BIOLOGY OF *TRIMERINA MADIZANS,* A PREDATOR OF SPIDER EGGS (DIPTERA: EPHYDRIDAE)

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Abstract.—Information is presented on the natural history, life cycle, and larval feeding habits of *Trimerina madizans* (Fallén), an uncommon but widely distributed species of Ephydridae. Females oviposit into the egg masses of the wetland spider *Hypselistes florens* (Cambridge), a species of Micryphantidae. Larvae destroy the spider eggs and form puparia within the silken covering of the egg masses. The developmental period from egg deposition to emergence of adults averages 23 days. Apparently there is only one generation a year in the latitude of northern Ohio. Information is given on a species of Ichneumonidae (Hymenoptera) whose larvae also attack the eggs of *Hypselistes.* The life cycle of *T. madizans* is contrasted and compared to that of *Scatella picea* (Walker), an algae-feeding, r-selected species of Ephydridae.

The family Ephydridae is generally considered to be closely related to the family Drosophilidae within the superfamily Drosophiloidea (Hennig, 1958; Griffiths, 1972). Although the two families differ in number of species (Drosophilidae, 2500 species; Ephydridae, 1400), both are widely distributed, have larvae that are largely microphagous, and have short generation times. Species of Drosophilidae are usually encountered in shaded woodland habits and have larvae that ingest mostly heterotrophic microorganisms such as yeasts and bacteria (Carson, 1971; Heed, 1968). In contrast, ephydrids are most commonly found in unshaded wetland habitats, and many species have larvae that feed primarily on autotrophic microorganisms such as algae (Deonier, 1972; Foote 1979). Interestingly, both families contain species that seemingly have abandoned the microphagous feeding habit and shifted to other nutrient sources. For example, predation on spider eggs occurs in both families. In Hawaii, larvae of species of the scaptomyzine genus *Titanochaeta* have been reported to attack the developing eggs of the spider family Thomisiidae (Wirth, 1952; Heed, 1968). Similarly, larvae of the ephydrid genus *Trimerina* prey on eggs of wetland spiders belonging to the family Micryphantidae in both Europe (Becker, 1926) and North America (Scheiring and Foote, 1973).

The present paper outlines the life cycle, describes the larval feeding behavior, and presents natural history observations of *Trimerina madizans* (Fallén). Additionally, a contrast is drawn between *T. madizans,* a highly specialized and probably K-selected species, and *Scatella picea* (Walker), a very trophically generalized and r-selected taxon within the family Ephydridae.

LIFE HISTORY

The genus *Trimerina* was established by Macquart (1885) for *Notiphila madizans* Fallén, a species originally described in 1813. The genus has remained

monotypic. It has a holarctic distribution, with records available for Europe (Becker, 1926; Dahl, 1959) and North America (Wirth, 1965). In the Nearctic Region, *T. madizans* has a transcontinental distribution, ranging from Ontario to Saskatchewan and Montana, south to New York, Colorado, and California. The genus is currently placed in the tribe Psilopini of the subfamily Psilopinae (Wirth, 1965).

Adults of *T. madizans* have been found most commonly in open wetlands having dense stands of herbaceous vegetation. In Scandinavia, Dahl (1959) recorded this species as uncommon in moist meadows, and Scheiring and Foote (1973) reported it as being relatively rare in the sedge-meadow habitat in Ohio. All habitats in which adults of *Trimerina* were found possessed dense growths of herbaceous reed-like vegetation. In northeastern Ohio, adults were swept from stands of broad-leaved cattail (*Typha latifolia* L.), bur-reed (*Sparganium eurycarpum* Engelm.), and sedges (*Carex* spp.). Other species of Ephyridae commonly collected with *Trimerina* adults belonged to the genera *Hydrellia* and *Notiphila*. The host spider deposits its egg masses on flattened herbaceous stems and leaves, usually 0.5–1.0 m. above the substrate (Fig. 1).

Females held in laboratory breeding chambers had a longevity that ranged between 30 and 80 days and averaged 57 days (n = 12), (Table 2). Males usually died before females and had an average longevity of 40 days (n = 5). None of the reared females mated or oviposited, so no information is available on the pre-mating or pre-ovipositing periods. The only information on fecundity is that a female, which was collected in nature on June 15, 1979, contained 20 recognizable eggs. Repeated dissections of reared females varying in age from 5 to 25 days revealed no developing eggs in the ovarioles or any sign of ovarian activity. These results, coupled with the failure to find infested spider egg masses in nature during late summer, suggest that *T. madizans* is univoltine. Adults probably overwinter, become active in late April and May, and begin ovipositing in late May and early June. Adults emerging from summer-formed puparia apparently enter into a reproductive diapause that lasts until the following spring.

Eggs were found beneath the silken covering of egg masses deposited by the marsh-inhabiting spider *Hypselistes florens* (Cambridge), a species of the family Micryphantidae. Apparently females of *Trimerina* are rather specific as to their oviposition site, as neither eggs nor larvae were encountered in egg masses of other species of spiders that occurred in the habitat. For example, no eggs were found in 15 egg masses of *Hyposinga variabilis* (Emerton), a small species of Araneidae that was frequently abundant in the same habitats in which *Hypselistes* occurred. Infected egg masses of *Hypselistes* were easily recognized by the presence of small, slit-like oviposition scars on the silken covering of the mass (Fig. 3). These slits were almost always located at either side of the egg cluster, and no eggs were found lying within the egg cluster itself. Only one egg was found below each slit, although the number of slits per egg mass was quite variable. The number of fly eggs present per infested egg mass varied from 1 to 7 and averaged 3.0 (n = 6). Occasionally, no egg was found below a slit, suggesting that false oviposition had occurred. Each egg was somewhat ovoid in shape, white in color, and lacked any sort of recognizable chorionic pattern. The incubation period for six eggs lasted two days. Newly hatched larvae moved away from the egg shells to the cluster of spider eggs and began feeding.

The infestation rate of spider egg masses sampled in northeastern Ohio was
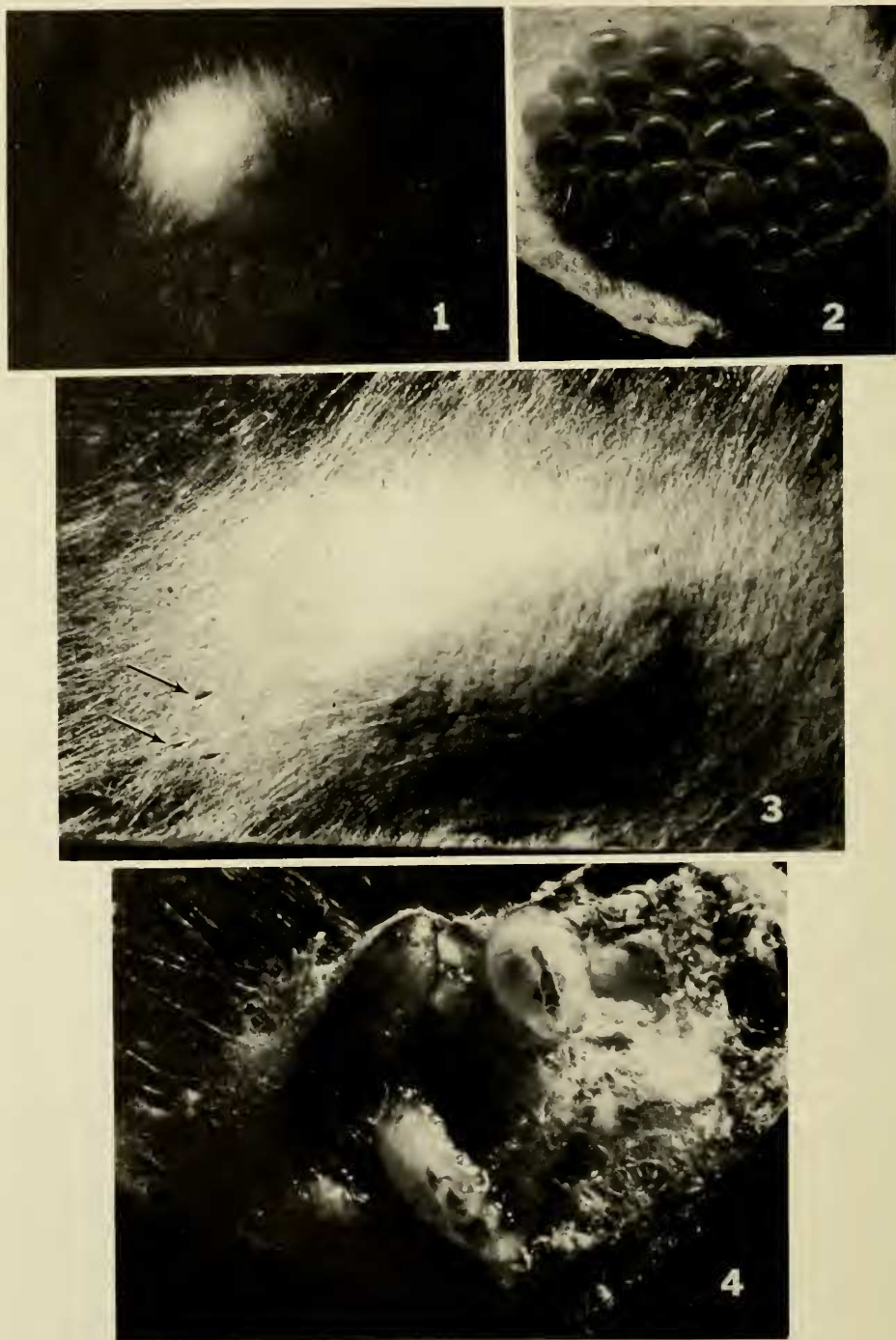
Figs. 1–4. 1, Egg mass of the spider *Hypselistes florens* on cattail leaf. 2, Egg cluster of *H. florens*. 3, Ovipositor scars of *Trimerina madizans* on spider egg mass. 4, Larvae and puparium of *T. madizans* within spider egg mass.

Table 1. Infestation rates of two spider egg predators.

Week of (1979)	Number of Egg Masses Collected	Infested by *Trimerina* (%)	Infested by Ichneumonid (%)
June 17	7	1 (14.3)	2 (28.6)
June 24	34	2 (5.9)	1 (2.9)
July 1	63	3 (4.8)	22 (34.9)
July 8	49	0 (0.0)	27 (55.1)
July 15	36	6 (16.7)	13 (36.1)
July 22	26	0 (0.0)	14 (53.9)
July 29	2	0 (0.0)	0 (0.0)
Aug. 5	0	—	—
Aug. 12	8	0 (0.0)	4 (50.0)
Aug. 19	5	0 (0.0)	2 (40.0)
Totals	230	12 (5.2)	85 (37.0)

quite variable, ranging from 0.0 to 16.7%, and averaging 5.2% (Table 1) during 1979 (230 egg masses examined). Infested egg masses were restricted to the period between June 17 and July 18, even though a few egg masses were found as late as mid-August.

All of the developmental stages were completed within the egg mass (Table 2). The larval period ranged from 7 to 10 days and averaged 8.6 days (n = 7). The pupal period varied from 12 to 14 days and averaged 12.7 days (n = 3). The number of *Trimerina* larvae and/or puparia (Fig. 3) per infested egg mass varied from 1 to 6 and averaged 3.1 (n = 13). The number of spider eggs in uninfested egg masses (Fig. 2) ranged from 28 to 51 and averaged 35.2 (n = 5).

The number of spider eggs destroyed by the feeding of *Trimerina* varied according to the number of larvae present in an egg mass. In general, if two or more larvae were present all of the eggs were consumed (Fig. 4). If only one *Trimerina* larva was present, at least one-third of the eggs remained uneaten. The data suggest that an individual larva requires at least six eggs to complete larval development. An egg complement of 35, the average number recorded for field-collected egg masses, thus would permit the development of four or five larvae.

The egg masses of *Hypselistes* were also utilized by larvae of Phoridae (Diptera) and Ichneumonidae (Hymenoptera). As Table 1 indicates, the most important insect enemy of the egg masses was *Gelis* sp., an ichneumonid, which infested 85 of 230 (37%) masses that were collected in northeastern Ohio during 1979. In contrast, only 12 of the 230 (5.2%) contained larvae and/or puparia of *Trimerina*, and none was infested by phorid larvae. Results in other years were similar except for an occasional occurrence of an undetermined species of Phoridae. However, in no sample did the phorid infestation rate exceed 2.0%.

Only rarely were egg masses doubly infested. Out of a total of 312 egg masses collected over a four-year period, only two were encountered that contained immature stages of both *Trimerina* and the ichneumonid. On May 22, 1982, an egg mass was obtained from a cattail leaf that contained two nearly mature larvae of *Trimerina* and one newly hatched ichneumonid larva. There were no viable spider eggs remaining in the mass, and the ichneumonid larva died within two days.

Table 2.   Life history data for *Trimerina madizans*.

Characteristic	n	Range	$\bar{x}$	SD
Adult longevity	7	30–80	57.1	20.0
Incubation period	6	—	2.0	—
Larval period	7	7–10	8.6	1.0
Pupal period	3	12–14	12.7	1.2

The *Trimerina* larvae formed puparia and eventually emerged as adults. On May 26, 1982, an egg mass was collected that contained five *Trimerina* and three ichneumonid eggs along with 38 apparently viable spider eggs. Three of the *Trimerina* eventually became adults, but all of the ichneumonid larvae died shortly after hatching. Available data suggest that although oviposition by one species of egg predator is not inhibited by the presence of eggs, larvae or puparia of a second species, only one species of predator can complete larval development within one egg mass. The reason for this phenomenon remains unknown, but it did not appear that there was any direct interference or attack by one species of larva on the developmental stages of the second species. The relatively high infestation rate shown by the ichneumonid compared to that of *Trimerina* (37 vs. 5%) implies that the wasp is more successful in locating egg masses and ovipositing within them.

The oviposition scars of the ichneumonid were easily distinguished from those of *Trimerina* in that they were much smaller and resembled pin pricks rather than elongate slits. Additionally, they tended to be more widely scattered over the surface of the silken covering of the egg mass and not concentrated towards either side as was true with *Trimerina*. The greatest number of unhatched ichneumonid eggs found in an egg mass was four, although several egg masses showed evidences of multiple oviposition probes. Up to 22 apparent oviposition scars were found in one egg mass. As in *Trimerina*, larval development of the ichneumonid took place entirely within the egg mass, with most or all of the spider eggs being consumed. Mature larvae subsequently spun cocoons within the egg mass. The larval period lasted eight days; the pupal period, six days in the one larva whose development was monitored. Although evidence is scanty, it appears that the ichneumonid is multivoltine. The rate of infestation seemingly increased during June and into July, whereas *Trimerina* levels decreased (Table 1).

The only indication that the immature stages of *Trimerina* were being attacked by parasitoid Hymenoptera was the discovery of two fly puparia that each contained a larva of an undetermined species of wasp. There was no evidence that the spider that deposited an egg mass presents any danger to ovipositing *Trimerina*, as the egg masses are not guarded or even tended by the female spider. Obviously, the timing of oviposition is critical for females of *Trimerina*, as the spider egg masses are suitable for larval development for only a restricted period of time. The incubation period of the spider eggs ranged between 10 and 15 days. It is very doubtful if first instar or even second-instar larvae can cope with newly hatched spiderlings, even though young spiders remained within the egg mass for one to three days after hatching. In contrast, third-instar larvae were seen preying

Table 3. Comparative life history data for two species of Ephydridae.

Character	Trimerina madizans	Scatella picea*
Adult longevity	57.1+ days	28.0 days (original data)
Fecundity	20?	310.5
Incubation period	2.0 days	1.9 days
Larval period	8.6 days	6.1 days
Pupal period	12.7 days	4.8 days
Gens./year	1?	Many
Larval food	Spider eggs	Algae
Habitat	Stable	Unstable

* Data obtained from Connell and Scheiring (1982).

upon spiderlings remaining with the egg covering. To ensure successful completion of larval development females of *Trimerina* probably must oviposit within the first four days after the spider egg masses are deposited.

DISCUSSION

Many if not most species of Ephydridae are best categorized as being r-strategists as defined by Pianka (1970). Certainly those species occurring in physically unstable and temporally varying shoreline habitats that are subject to repeated and unpredictable flooding must allocate most of their available energy to reproductive efforts. Thus, such species as *Scatella picea* that are associated with the mudshore habitat (Scheiring and Foote, 1973) are relatively short lived as adults, have very high fecundities, abbreviated developmental times, are trophically generalized, and show high vagility (Connell and Scheiring, 1981, 1982). In contrast, trophic specialists must expend a considerable fraction of their energy in searching for a suitable food resource that frequently is uncommon and relatively hidden. As a result, certain components of the life cycle have been modified. In *T. madizans*, for example, the adult life span is somewhat extended, egg production is greatly curtailed, the developmental period is lengthened, and the number of generations produced per year is dramatically reduced. Table 3 compares certain life history traits for *S. picea* and *T. madizans*. It is obvious that the two species are dramatically different in such life cycle components as adult longevity, fecundity, pupal period, and number of generations produced per year. Apparently these two species represent endpoints on the r-K continuum in the family Ephydridae, although a detailed study of the population biology of *T. madizans* that could be compared and contrasted to the demographic data available for *S. picea* is sorely needed.

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